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DIFFERENTIAL PREY SELECTION FOR THE SEX OF OFFSPRING IN THE CICADA KILLER *SPHECIUS SPECIOSUS* (HYMENOPTERA: SPHECIDAE)

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Abstract.—Data originally obtained by Dow (1942) were reanalyzed and showed that female cicada killers, *Sphecius speciosus,* knew, in advance of the hunt, the sex of the egg they would lay. Consequently, they provisioned 12 male cells in most cases with a single cicada of the smaller species *Tibicen canicularis,* and more often than not the sex of the cicada was the smaller male. Each of the six female cells was provisioned with two female cicadas of both the larger and smaller species *T. canicularis* and *T. lyricen* 50% of the time. The finding by various observers that more female cicadas were captured than male cicadas is now explained because most female cells receive two large female cicadas because they are the heavier sex. Male cells nearly half the time receive small female cicadas. Weight rather than number of prey is critical since some female cells as shown by Dambach and Good (1943) were provisioned with a single large female cicada of *T. lyricen* while others received three cicada prey. Two male cells were provisioned with two cicadas, a male and female of the lighter species. Some female cicada killers specialize in producing all male nests; others produce both sexes and possibly all female nests.

According to Krombein (1967) female wasps or bees know in advance before storing the cell with food, the sex of the egg which she will place in the cell prior to sealing it. With the Vespidae where the egg is laid before the cell is provisioned, the wasp still controls and knows the sex of the egg she has laid, because she brings in a large number of caterpillars if it is to be a female or a small number if it is to be a male. Krombein further stated that females of all vespid wasps and most sphecid wasps and bees, lay a series of female eggs in larger cells before a series of male eggs in larger cells before a series of male eggs in nests where both sexes are produced. Krombein was speaking in connection with solitary wood-nesting predaceous wasps and bees. However, there are reasons to believe that this remains true of many ground-nesting sphecid wasps and bees. Evans (1971)

stated that production of females in larger cells containing more prey is probably common in ground nesters, though it has been clearly demonstrated only in *Sphecius speciosus* (Drury) (Dow, 1942). However, Dow did not comment on size differences, if any, between cells. Evans (1971) in studying *Cerceris fumipennis* Say found that cells were of two sizes: Large cells 25 to 30 mm long and small cells approximately 20 mm long. When provisioned with large buprestids (*Dicera*), large cells typically contained four; small cells, two. When provisioned with *Argilus,* large cells contained 16 to 32; small cells, 8 to 12. Large cells contained larger larvae that made larger cocoons. It seemed probable that the small cocoons would produce males and the large ones females. The female *C. fumipennis* is considerably larger than the male, and there is relatively little overlap in size. Evans (1971) found that the majority of nests were provisioned with *Argilus* and that the use of the larger buprestids was mainly confined to a few females that took them in considerable numbers, indicating that they learned where to find the larger buprestids.

In the cicada killer, male eggs are typically provisioned with one cicada, and female eggs are typically provisioned with two cicadas (Dow, 1942).

Usually, there are more than one species of annual cicada in an area, and female wasps prey upon more than one species (Dow, 1942; Dambach and Good, 1943; Lin, 1979).

Examination of Table 1, data taken from Dow (1942), shows that two species of cicadas were preyed upon in Berkley, Massachusetts, *Tibicen canicularis* and *Tibicen lyricen*. The male sex is often the lighter, and *T. canicularis* is a smaller species than *T. lyricen*. To get an estimate of the weights of the cicadas, Dow captured a specimen of each cicada and found the male *T. canicularis* to weigh .93 g, the female 1.12 g and the male *T. lyricen* to weigh 1.39 g, the female 1.94 g.

Table 1 shows that when provisioning 12 male cells, only a single prey species was used in each cell with the exception of two which each received a male and a female cicada of the smaller *T. canicularis*. Also, the sex of the cicada was male in six cells, and female in four cells; and, of course, in two cells both male and female. The prey species in nine of the twelve cells was the small *T. canicularis*. Of the three exceptions, two were the lighter males of *T. lyricen* and only one was a female of the latter species. Regarding the female cells, if selection of prey by the female wasp was not the case, then the probability of the contents of the six female cells would have been exceedingly low. Each of these six cells first received a female cicada; and then again, each received an additional female cicada making the probability of consecutively receiving twelve female cicadas. The female cicada received was, in half the cases, the smaller species and in half the cases, the larger species. Thus, two cells received two *T. canicularis,* and two cells received two *T. lyricen,* and two cells received one of each species.

Table 1. Data pertaining to the cells from which adults were reared.[1]

Number of cicadas in cell	1	1	1	1	1	1	1	1	1	1	2 ?	2	2	2	2	2	2	2
Tibicen canicularis	♂	♂	♂	♂	♀	♀	♀				♂,♀	♂,♀	♀,♀	♀,♀	♀	♀		
Tibicen lyricen								♂	♂	♀					♀	♀	♀,♀	♀,♀
Length of cocoon (mm)	24.0	29.5	29.5	29.5	29.5	29.5	31.0	32.0	31.0	32.0	31.0	32.0	40.0	39.0	40.5	39.5	40.5	40.5
Weight of cocoon (g)	0.67	1.05	1.30	1.25	1.14	1.28	1.37	1.39	1.59	1.48	1.30	1.62	2.96	2.96	3.40	3.16	3.15	3.33
Weight of adult (g)	0.13	0.25	0.28	0.43	0.27	0.36	0.38	0.36	0.42	0.39	0.43	0.44	0.63	0.69	0.81	1.09	0.61	1.06
Sex of adult	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♀

[1] Table modified from Dow, 1942.

The weight of the cocoon in the six female cells ranged from 2.96 g to 3.40 g. In the cicada killer, there is seldom overlap of size, and females are considerably heavier than males (see Lin, 1979, for an exception). The weight of the cocoon in the 12 male cells including the two provisioned with two cicadas ranged from .67 g to 1.62 g. The weight of the adult males ranged from .13 g to .44 g, the weight of the adult females ranged from .61 g to 1.09 g.

The cocoon weights are rough estimates of the prey weights and the adult weights (Table 1). When the female cocoon weights were divided in half for comparison with those male cocoons which received one prey species, they were as follows: 1.48 g, 1.48 g, 1.58 g, 1.58 g, 1.67 g, and 1.70 g. Only two male cocoon weights weighed as much or more than one-half a female cocoon. These were a male cocoon whose prey was a female *T. lyricen* which weighed 1.48 g, the two lowest values of the female cocoon weights; and a male cocoon provisioned with a male *T. lyricen* weighing 1.59 g. With the exception of these two cases, one-half the weights of all cocoons destined to become females weighed more than all cocoons destined to become males. In the cases of the two exceptions, it is quite possible that the first female prey species in each of the female cells weighed more than just one-half the female cocoon and consequently weighed more than the male cocoon prey. These findings generally support the view that heavier female prey individuals were used when rearing a female wasp as opposed to a male wasp. In the two cases of male cocoons each receiving a male and female cicada, one-half the weight of the cocoons was only .81 g and .65 g, respectively.

The data presented here confirm that females know the sex of the egg she will lay before going on the hunt; it is clear that the hunting female engages in prey selection of a complex sort. If she is to lay a female egg, she hunts for two female cicadas, and presumably specimens on the heavier side, judging from the species of cicada, its sex, cocoon weight, and the adult weight (see Table 1). If she is to lay a male egg, she hunts for lighter prey, this being in most cases the capture of the smaller prey species *T. canicularis* and often the lighter male sex is "selected."

Davis (1920) found that more female cicadas were taken as prey than male cicadas and in doing so called attention to the erroneous idea prevalent among naturalists that *Sphecius* secure its prey by hunting only singing males. Dow (1942) also found more female prey, 24 males to 44 females; and Dambach and Good (1943) found the same: of 703 captured cicadas, only 204 were males. The writer studied a population of *Sphecius* in Pineville, Louisiana in 1977 and found eight of ten cicadas captured by *Sphecius* to be female. Various hypotheses have been put forth to explain why more female cicadas are taken than male cicadas.

According to Dambach and Good (1943), "The disproportionate sex ratio

may be due to the greater susceptibility of females to the hunting system employed by the wasp. Male cicadas are probably more readily disturbed than are ovipositing females."

Dow (1942) has suggested that, ". . . it might be that the females are less active (hence more susceptible to capture), longer lived (therefore more abundant during the nesting period of the wasp), or more likely to occur where the wasp will find them. There is also the possibility that there is some selection on the part of the wasp."

The last hypothesis apparently provides the answer to the question. Data presented here indicate that it is indeed the case that there is selection on the part of the wasp, as Dows' data show (Table 1). Each female cell was provisioned with two female cicadas, one-half being the heavier *T. lyricen*. Male cells were typically provisioned with one cicada, the lighter female of *T. canicularis* or male cicadas which are also light; only three of twelve male cells received a *T. lyricen*. Thus, Table 1 shows 18 captured female cicadas as compared to eight male cicadas. The reason for the female bias in cicadas is now clear; it is due to the fact that female cells each receive typically two female cicadas because they are heavier, while male cells receive, probably depending on chance, approximately one-half male and one-half lighter female cicadas; there were 8 ♂♂:6♀♀ cicadas in the male cells.

Dambach and Good (1943) found that 47 cells containing small larval cases were found to be provisioned with one cicada. Cells containing large larval cases were found to have been provisioned with two cicadas in 19 cells and with three cicadas in five cells. Only two large larval cases were found with single cicadas, and each of these had a large female *T. lyricen*. Presumably, small larval cases were male and large ones female. Dow (1942) also found three cells provisioned with three cicadas each; however, none contained cocoons.

It would be a decided advantage for the female wasp to know in advance the sex of the egg to be laid so that especially in the cicada killer enough prey of the right sex and hence weight are brought in for the larger female host. If this were not the case, a female cell might receive one or two male cicadas possibly also of the lighter species *T. canicularis* as prey, and this would not be sufficient for rearing an adult female. Under ordinary conditions a female cell must receive two female prey of sufficient weight to rear an adult female. As Dambach and Good's (1943) data already indicated it is not the quantity of prey per cell which is of major importance but the approximate weight of the prey which the cell holds. According to Dambach and Good (1943): ". . . in hunting, the wasp approaches a tree or shrub and slowly circles closely about the trunk, gradually working its way up through the limbs and branches. It sometimes alights on the bark and continues the search on foot."

During the summer of 1964, I saw numerous instances of females circling the lower trunks of trees in Lawrence, Kansas. Dambach and Good (1943) cited the method of attacking the cicada when located. Mr. Conrad Roth witnessed the capture of a *T. pruinosa* at close range. "The wasp darted backward and forward in front of the cicada several times meanwhile bending the tip of the abdomen downward and forward. It then hit the cicada viciously and injected the sting." The cicada buzzed shrilly and immediately ceased struggling. "The wasp managed to hold its prey to the limb of the tree and pulled it up on the top side of the limb." The wasp turned the cicada over on its back, grasped it in the usual carrying position and flew off with it. Color probably plays a major role in locating the cicada. In 52 instances in the Parade Grounds in Brooklyn, New York, when a female dropped or was deprived of her prey, she was seen to fly repeatedly backward and forward over pieces of green glass apparently mistaking them for prey before finding her prey. Females never showed such responses to brown glass or other objects. A boy who assisted me in my work in the Parade Grounds had captured a large green tobacco horn worm whose color is similar to a cicada's and left it in a small jar in his backyard across the street from the Parade Grounds. A female *Sphecius* entered the jar, and I was shown the jar containing the captured female wasp and the horn worm. Dambach and Good (1943) reported an account by J. N. Knull that *Sphecius* may take its prey in full flight. They point out, however, that this is not the usual method as evidenced from the apparent safety enjoyed by cicadas observed flying to and from trees 10 feet to 25 feet in height while cicada killers were busy searching the lower limbs in the usual methodical manner. Dambach and Good (1943) suggested that should a cicada attempt escape by flight after being located, pursuit and probably capture would result. Thus, by carefully locating its prey, a female *Sphecius* would probably be able to "judge" its weight so as to bring back a light cicada for male prey and a heavy cicada for female prey. While Davis (1920) showed that *Sphecius* does not secure its prey by hunting only singing males, he did not, however, prove that sound is sometimes not used by *Sphecius*. Arnold (1929) reported on the South African *Sphecius milleri* which preys on large cicadas such as *Munza furva, Platypleura quadraticollis, P. lindiana* and *P. marshalli* which live largely on small mopanin trees (*Copaifera mopani*). The *Sphecius* circles round these trees and makes a sudden swoop at its prey and stings it on the ground. It is found that when a *Sphecius* comes within a foot or so of the trees, the vociferous din of the cicadas ceases quite suddenly, suggesting that *Sphecius* might sometimes locate male prey by their song.

Some female cicada killers in the Brooklyn populations produce all male nests, and others produce nests containing both sexes. Some females may produce all female nests (Lin and Michener, 1972). In this regard, Savin (1923) found the greater number of cells uncovered contained two cicadas.

All females discussed have been mated (Lin and Michener, 1972). Since females are considerably larger than males and there is almost no overlap in sizes, the sex of the offspring of various nests can be determined by the size of the emergence hole made by the eclosing wasps the following season.

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